DYNAMICS OF UNDERSTORY BIOMASS IN SITKA SPRUCE–WESTERN HEMLOCK FORESTS OF SOUTHEAST ALASKA[1]

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Abstract. Understory vegetation undergoes successional stages during the 1st 300 yr after logging or fire disturbance in the coastal *Picea-Tsuga* forests of southeast Alaska. Residual shrubs and tree seedlings increase their growth within 5 yr after overstory removal. Understory biomass peaks at 5 Mg·ha^{-1}·yr^{-1} $\approx$15–25 yr after logging. Shrubs and herbs are virtually eliminated (<0.1 Mg/ha) from the understory after forest canopies close at stand ages of 25–35 yr. Bryophytes and ferns dominate understory biomass during the following century. An understory of deciduous shrubs and herbs is reestablished after 140–160 yr. Thereafter, biomass of the shrubs, herbs, and ferns continues to increase, while bryophyte biomass and tree productivity decline. Departures from this developmental sequence are related to unusual types of stand establishment, soil, microclimate, or disturbance.

The development and duration of the depauperate understory that succeeds canopy closure in southeast Alaska is closely related to the canopy structure of shade-tolerant *Tsuga* forests with their high foliar biomass. In young-growth forests (<100 yr), the decline in understory development immediately after canopy closure is significantly associated with tree basal area and percentage of tree canopy cover. In old-growth forests, in contrast, understory biomass is correlated with mean tree diameter, age, and volume. It is hypothesized that understory development over the chronosequence responds primarily to changes induced in the light environment by developments in the forest canopy.

Maintenance of the most productive forests in the aggradation stages of development (0–100 yr) through forest management will minimize the development of a productive vascular understory and thus deprive herbivores of forage during 70–80% of the forest rotation.

Key words: old-growth forests; Picea sitchensis; secondary succession; southeast Alaska; Tsuga heterophylla; understory biomass; understory-overstory relationships; understory production; wildlife habitat.

INTRODUCTION

In the forest ecosystems of the Pacific Northwest as far north as southeast Alaska, many sites escape destruction by fire, wind, and other agents; consequently, plant succession may continue over centuries (Hemstrom 1979, Waring and Franklin 1979). These later stages of succession have rarely been studied by ecologists, yet they offer the best opportunities to test hypotheses on successional development and to understand the transition to the "climax" or the dynamic equilibrium of the old-growth system (Whittaker 1953, Odum 1969, Bormann and Likens 1979).

Vegetative changes are usually documented by estimating ground coverage by various plant species. The contributions of individual species to ecosystem functioning can be evaluated more precisely by measuring plant biomass or net primary production (Whittaker 1975). Such measurements were originally tedious and time consuming, suitable only for a few, intensively studied sites. Now, however, dimensional analysis has made it possible to estimate plant production more quickly and efficiently, yet with sufficient accuracy to detect subtle changes in understory abundance (Whit-

taker 1966, Brown 1976, Ohmann et al. 1976, Grier and Logan 1977).

Most studies of understory productivity have been conducted over an insufficient time span to address questions of changes in ecosystem functioning and structure as forests mature to the old-growth stage of succession (Wallmo and Schoen 1980, Franklin et al. 1981). Most conceptual and empirical models of succession have also failed to address details of understory dynamics during these later stages of succession (Bormann and Likens 1979). Information on understory productivity is essential to portray accurately the subtle patterns of change in understory dominance and species importance (Whittaker 1975). Studying understory productivity on sites representing a protracted successional sequence and a wide range of environmental conditions would provide a broader basis for evaluating both the factors influencing understory productivity and the applicability of the "climax" concept to specific types of mature forest ecosystems.

The objectives of this study were twofold: first, to document both short- and long-term changes in understory biomass over a range of site conditions in southeast Alaska; second, to evaluate environmental factors associated with understory change over the chronosequence. By studying these long-term successional patterns, it was hoped that relationships between
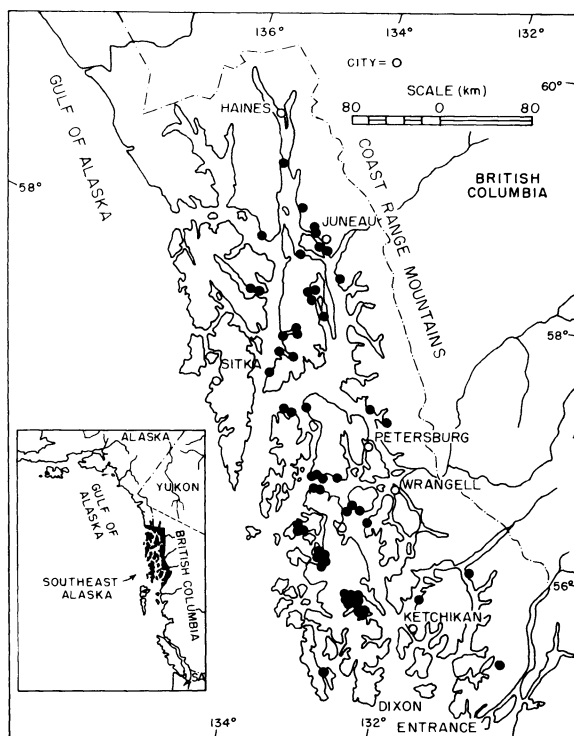
FIG. 1. Location of study plots (•) in southeast Alaska. (Inset) Southeast Alaska in relation to the Pacific Northwest.

vegetation of different ages and on different sites in the region would be clarified.

THE STUDY AREA

Geography and climate

Southeast Alaska is a cool temperate region of steep, glaciated mountain ranges, fjords, muskegs, and fog-enshrouded coniferous forests. For this study, the region is defined as that area from Haines (59°N, 136°W) 700 km southeast to Dixon Entrance (54°30'N, 130°W) (Fig. 1). Its average width is about 190 km.

Despite its high latitude, southeast Alaska has a cool, wet maritime climate as a result of the North Pacific warm stream. In general, the climate of the region can be distinguished from those further south by its heavy annual precipitation (200–600 cm) and cooler growing season. The summer drought, which so strongly affects the dynamics of coniferous forests in the Pacific Northwest and southern British Columbia, does not clearly affect this region (United States Forest Service 1974, Waring and Franklin 1979).

Mean monthly temperatures range from 13°C in July to 1° in January. On the average, 1200 degree-days above 5° occur in the region (Farr and Harris 1979). The mountainous terrain of this region causes wide variations in climatic conditions (Andersen 1955). Precipitation is generally heaviest on the outer coastline,

declining to the east until one reaches the Coast Range foothills, where it again increases. Wind patterns and other factors can also dramatically influence local rainfall and temperatures within the region.

Geology and soils

The physiographic features in southeast Alaska are the result of the northwest orientation of faults, bedrock strikes, and lineaments. The overall geological pattern can be summarized as a northwesterly eugeosyncline with Paleozoic rocks dominating the central lowland provinces. More erosion-resistant batholithic rocks of Mesozoic age dominate the mainland and outer coastal flanks of the mountain system (Buddington and Chapin 1929, Brew et al. 1966).

Little detailed geological information is available for the sites sampled in this study. The earlier geological descriptions of southeast Alaska were based primarily on shoreline mapping. More recent studies have used aerial photos with some spot checks. Detailed geological maps from on-the-ground surveys have been developed for only a few areas (United States Geological Survey 1977).

Soils in southeast Alaska are generally young (200–10 000 yr old), shallow, and poorly developed (Crocker and Major 1955, Collins 1974). Compact glacial till is extensive up to elevations of 500 m in major river valleys, exerting a great influence on drainage conditions and forest development in the region (Swanston 1969). Most of the soils in the study area are derived from this ablation till (Collins 1974). Because of the till overburden and the heavy annual rainfall, bedrock usually plays a lesser role in soil chemistry than in more southerly regions (Heilman and Gass 1974). The soil mineral fractions are generally low in nutrients because of a lack of weathering of bedrock and glacial till (Swanston 1974).

Some of the best-developed soil structures occur on fine silt and clay sediments of extensive marine terraces up to 150 m in elevation. Soils derived from marble and limestone with extensive subsurface drainage tend to have the lowest proportion of poorly drained areas and give rise to some of the most productive and best developed forests (Jacques 1973). In contrast, soils of hard intrusive rocks have a higher percentage of poorly drained areas and less productive forest vegetation (Collins 1974).

Most of the soils on forested sites of southeast Alaska are classified as spodosols, having thin A2 and B21 horizons, extremely to very strongly acid sola, weak structure, and thixotropic properties (Heilman and Gass 1974). These soils strongly attract and hold water, remaining moist throughout the year (Patric and Stephens 1968).

A soil classification system keyed to tree-growing potentials was used in this study in order to integrate understory growth with the environmental character-

istics associated with soils.[2] Five major forested types are defined on the basis of drainage characteristics, parent material, and depth. The first type (F1) represents the modal soil for well-drained, low-elevation sites having the highest tree productivity classes. The second type (F2) is distinguished by having <25 cm of mineral soil. The third type (F3) includes soils on coarse glacial or volcanic deposits. The last two types (F4, F5) have somewhat poor and poor drainage conditions, respectively. In this study primary emphasis was placed on well-drained sites, where the most productive forests develop. The F2 and F4 soil types were sampled only where suitable F1 sites were not available for a given age class.

Vegetation

Previous studies.—No comprehensive studies have been made of the structure or composition of forest vegetation in southeast Alaska. Early studies were descriptive and directed primarily at the growth and abundance of the two principal forest trees: Sitka spruce, *Picea sitchensis* (Bong.) Carr., and western hemlock, *Tsuga heterophylla* (Raf.) Sarg. (Taylor 1929, 1932b, 1933, 1934, Heintzleman 1949). (Nomenclature in this article follows Hulten [1968] for vascular plants, Hale and Culberson [1970] for lichens, Worley [1970a] for liverworts, and Worley [1970b] for mosses, except where more recent nomenclatural changes have been published.)

Studies of successional dynamics in southeast Alaska have centered on revegetation after glaciation (Cooper 1923a, 1923b, 1939, 1956, Lawrence 1958, Reiners et al. 1971). Secondary succession has received little attention in this region. Taylor (1929, 1932a, b) and Harris (1974) provide the best general descriptions of the early stages of plant succession after logging. Forest growth and accumulated volume for the first 150 yr after cutting have been studied by Taylor (1934) and Taylor and Godman (1950). There are no published studies summarizing the dynamics of understory vegetation during this time span.

Description.—Approximately 60% of the land in southeast Alaska is forested. The remaining area is alpine, muskeg (bog), or riparian (United States Forest Service 1978). Well-developed, closed-canopy forests occur from sea level to ≈600 m in elevation. *Tsuga-Picea* forests usually occur at low elevations on well-drained soils as a mosaic with muskegs and other wetlands (Neiland 1971). This forest type, which comprises the majority of closed-canopy forests in the re-

gion, is the subject of this study. The type encompasses the *Picea sitchensis, Picea sitchensis-Tsuga heterophylla, Tsuga heterophylla-Picea sitchensis,* and *Tsuga heterophylla-Thuja plicata* communities defined by Viereck and Dyrness (1980).

Of these forests, 75% are "old growth" (>150 yr old), while most of the remainder are of windthrow or logging origin (United States Forest Service 1978). Fire has not been important in the ecology of these forests (Noste 1969, Harris and Farr 1974). Most of the disturbance to them is caused by infrequent high-velocity winds that blow down large patches of trees during fall or winter (Ruth and Harris 1979).

METHODS

Plot selection

Sixty plots ranging in elevation from 0 to 274 m, with nearly uniform slope and aspect, were selected (Table 1). These plots represented stand ages from 3 yr to ≈400 yr and ranged in size from 0.09 to 0.5 ha. The larger study plots were used for older forests in which variation in tree size and density was sampled more intensively. Within each age class, a range in soil, climatic, and geographic conditions was represented. For the younger forests, permanent plots stratified by age and tree site index were used. Forests <70 yr old, most of them of logging or fire origin, were easy to locate over a broad range of edaphic and environmental conditions. Older forests of similar origins and without evidence of subsequent disturbance were difficult to locate over this range of conditions. When a suitable plot of logging or fire origin was not available for an age class, forests of windthrow origin were sampled.

The selected plots were even-aged and homogeneous except in the oldest forests, where an uneven-aged structure predominated. Because the plots represented similar environments and histories, differences in vegetative structure and composition were presumed to be associated primarily with differences in age (Horn 1974).

Plot measurements

Measurements of forest structure and environmental variables were made during the summers of 1977 to 1979. A soil pit was dug at plots where a complete soils description was not already available, and soil structure, depth, drainage characteristics, and color were noted. Data on tree height, diameter, and age were obtained from the United States Forest Service for those sites used in previous studies. On the other plots, all trees >2.5 cm in diameter were measured at breast height to the nearest 0.5 cm. Heights and ages were measured on representative codominant trees at each plot. These data were then used to estimate tree volume, basal area, site index, and tree foliar biomass

TABLE 1. Understory biomass and environmental features of plots sampled in southeast Alaska.

Age*	Plot (no.)	Name	Origin†	Slope (%)	Aspect	Eleva-tion	Biomass (Mg/ha)	Production (Mg·ha⁻¹·yr⁻¹) Shrub	Herb	Fern	% basal area in— Picea	Thuja	dbh (cm)	Site index‡	Soil§	Parent material‖
3	9	Clark Bay I	L	30	SE	45	1.2	0.4	<0.1	0.2	...	...	...	...	F1c	V
8	25	Clark Bay II	L	10	SE	38	3.0	0.3	0.1	<0.1	...	...	...	...	F4c	T
10	44	Pt. Barrie II	L	0	0	30	9.5	3.7	<0.1	0.5	56	0	4.9	37	F1n	V
15	12	Douglas Bay	L	0	0	5	5.0	0.6	<0.1	<0.1	61	0	7.3	36	F1n	V
20	50	Pt. Vandeput	L	0	0	2	58.5	3.4	0.6	<0.1	7	0	3.5	37	F3n	B
21	52	Maybeso Valley	L	10	S	91	33.0	4.9	0.2	<0.1	25	4	6.6	40	F1c	T
21	7	Harris River	L	0	0	67	0.5	0.2	<0.1	<0.1	21	0	3.9	38	F1t	A
22	11	Thomas Bay	L	0	0	8	8.1	0.8	<0.1	<0.1	39	0	0.4	31	F3g	T
27	48	Shrubby Island	L	0	0	91	12.5	2.0	<0.1	<0.1	67	0	4.2	35	F1n	M
31	24	Tuxekan Island I	L	40	S	30	5.5	0.4	<0.1	<0.1	12	0	4.4	30	F1n	S
31	27	Tuxekan Island II	L	10	S	90	0.3	0.1	0	<0.1	66	0	8.1	38	F1n	S
34	2	Hood Bay II	L	47	W	31	<0.1	0	<0.1	0	57	0	23.3	39	F2r	L
37	49	South Zarembo	L	0	0	23	2.8	0.8	<0.1	<0.1	14	0	5.8	37	F1b	B
40	45	Saginaw I	L	0	0	46	0.2	<0.1	<0.1	<0.1	15	0	29.6	36	F1n	L
42	14	West Zarembo	L	0	0	7	<0.1	<0.1	<0.1	<0.1	83	0	16.2	42	F1b	B
44	33	Edna Bay I	L	0	0	30	3.1	<0.1	<0.1	<0.1	76	0	26.2	40	F1n	L
45	13	Agate Beach	L	0	0	7	1.1	0.2	<0.1	<0.1	23	0	7.3	31	F1b	B
45	29	Alder Creek I	L	0	0	30	0.2	<0.1	<0.1	<0.1	6	0	8.3	32	F1n	L
45	30	Alder Creek II	L	0	0	30	<0.1	<0.1	<0.1	<0.1	14	0	15.5	38	F1n	L
48	35	Edna Bay III	L	10	N	152	0.5	<0.1	<0.1	<0.1	26	0	13.8	37	F1n	L
51	4	Whitewater Bay	L	20	SW	30	<0.1	0	<0.1	<0.1	97	0	14.0	37	F1n	V
52	47	Pt. White	L	0	0	30	<0.1	<0.1	0	<0.1	36	0	12.6	33	F1n	M
53	32	Virgin Bay	L	30	SW	122	<0.1	<0.1	0	<0.1	20	0	17.7	40	F1n	S
58	31	Saks Cove	L	0	0	30	0.2	<0.1	<0.1	<0.1	27	0	26.6	36	F1n	V
59	19	Mission Cove	L	0	0	15	<0.1	<0.1	<0.1	<0.1	44	0	31.0	41	F1f	L
60	1	Hood Bay I	L	0	0	30	<0.1	0	<0.1	<0.1	12	0	21.8	37	F1n	L
64	41	Douglas Island	M	10	S	30	1.5	0.2	0.1	0.1	52	0	22.9	30	F4r	MT
69	43	Pt. Barrie I	L	20	S	33	0.1	<0.1	<0.1	<0.1	70	0	24.0	38	F1n	V
71	5	Karta River	F	20	E	30	<0.1	<0.1	<0.1	<0.1	43	7	18.3	33	F1c	T
71	6	Karta Lake	F	0	0	61	<0.1	0	<0.1	<0.1	43	7	17.4	33	F1c	T
72	23	Old Franks III	F	20	S	30	<0.1	<0.1	0	<0.1	28	49	7.9	20	F1n	S
72	26	Old Franks IIb	F	10	S	61	<0.1	<0.1	0	<0.1	52	0	20.2	37	F1n	S
72	36	Edna Bay IV	L	10	S	91	0	0	0	<0.1	66	0	8.9	29	F1n	L
72	21	Old Franks I	F	0	0	30	<0.1	<0.1	0	0	78	0	34.2	40	F1n	S
72	22	Old Franks IIa	F	0	0	30	<0.1	<0.1	0	0	5	66	16.7	23	F1n	S
90	60	Windfall Harbor	W	50	NE	91	2.4	0.2	0.2	0.1	54	0	33.8	30	F2n	V
90	54	Tenakee	F	20	S	5	0.2	<0.1	<0.1	<0.1	0	0	17.8	33	F2n	V
90	56	Killisnoo	L	0	0	5	0.1	<0.1	<0.1	<0.1	81	0	30.4	46	F1b	V
94	15	Eagle River	W	10	S	274	0.6	<0.1	<0.1	<0.1	9	0	22.1	27	F2n	V
95	61	Windfall Island	L	0	0	5	0.1	<0.1	<0.1	<0.1	63	0	36.7	38	F1b	B
96	46	Saginaw III	W	0	0	91	0.2	<0.1	<0.1	<0.1	11	0	29.8	33	F1f	L
100	51	Kindergarten Bay	F	10	S	15	0.1	<0.1	<0.1	<0.1	36	33	17.6	30	F2n	M
100	59	Young Bay	F	0	0	8	17.2	0.4	0.1	0.1	37	0	41.0	40	F1t	A
108	28	Bartlett Hospital	L	10	S	30	0.8	<0.1	<0.1	<0.1	4	0	29.9	37	F2n	V
138	58	Cannery Point	F	0	S	0	0.2	<0.1	<0.1	<0.1	56	0	36.4	22	F1n	M
142	57	Kanulku Bay	F	10	0	30	0.1	<0.1	<0.1	0	26	0	15.7	32	F2r	V
150	34	Dorn Island	W	0	0	5	0.9	<0.1	0.1	<0.1	46	0	34.5	27	F4c	T
150	63	Salisbury Point	L	0	0	6	2.3	0.3	0.1	<0.1	64	0	28.6	30	F1b	V
150	39	Chilkat Peninsula	W	20	SE	31	<0.1	<0.1	<0.1	0	42	0	27.3	31	F4c	T
154	55	Mitchell Bay	F	0	0	25	1.4	0.2	0.2	<0.1	17	0	36.8	37	F1n	M
187	20	Sullivan Island	F	30	SW	107	1.9	0.2	<0.1	0.1	26	0	34.5	30	F1n	V
188	40	Red River	W	10	NE	107	2.5	0.1	<0.1	<0.1	56	2	19.4	...	F1n	V
192	37	Clark Bay III	W	10	E	45	1.0	<0.1	0	<0.1	29	0	8.6	35	F1c	T
192	38	Clark Bay IV	W	10	E	45	0.7	<0.1	<0.1	<0.1	35	18	29.6	35	F1c	T
250	16	Limestone Inlet	...	60	N	61	1.4	0.2	0.1	0.3	...	0	39.2	...	F4c	V
250	42	Lemon Creek	...	20	E	46	6.0	0.7	0.1	0.1	0	0	35.2	...	F1n	M
300	62	Pack Creek	...	10	N	28	5.2	0.5	0.2	0.2	10	0	26.9	...	F4c	T
400	17	Shaheen I	...	0	0	46	0.5	<0.1	<0.1	<0.1	20	0	28.0	...	F1c	T
400	18	Shaheen II	...	0	0	46	0.6	<0.1	<0.1	0	0	0	24.8	...	F1c	T
550	53	Shaheen Creek	...	0	0	5	0.7	0.1	0.1	0.3	43	0	30.2	...	F1t	A

* Mean age of codominant trees. For the old-growth plots, actual time since disturbance may be much greater than indicated by these data.

† L = clearcut logged, F = fire, W = windthrow, M = mining disturbance.

‡ Predicted codominant tree height (m) at 100 yr.

§ Nomenclature follows Stephens, F. R., C. R. Gass, R. E. Billings, and D. E. Paulson. 1969. Soils and associated ecosystems of the Tongass. This 67-page report is available as ESA Supplementary Publication Service Document No. ESPS-8107. For a copy of this document, contact the author or order from The Ecological Society of America, Cornell University, Ithaca, New York 14853-0239 USA.

‖ S = sandstone or mudstone, V = igneous rock, M = metamorphic, T = glacial till, L = limestone or marble, A = alluvium, MT = mining tailings, B = beach sands.

from prediction equations (Taylor 1934, Chambers and Foltz 1979, Gholz et al. 1979). The biomass equations for *Tsuga heterophylla* from Gholz et al. (1979) were derived from trees sampled in the Cascades of the Pacific Northwest. Thus, they probably gave overestimates for Alaskan trees but were assumed to be useful for a general index of relative foliage mass.

Vegetative structure and biomass were documented by establishing 60 1-m² quadrats in clusters of four in a systematic grid at each site. The basal diameters of all shrub shoots and the lengths of fern fronds and selected herb shoots (those species whose biomass can be precisely estimated from plant length) were measured in each 1-m² quadrat. Cover class was estimated for all plant species or species groups encountered within a 0.1-m² rectangular frame placed in the center of each plot (Daubenmire 1959). In forested plots, cover class was estimated only for understory plants (herbs, mosses, ferns, liverworts, trees, and shrubs) whose basal diameters were <2.5 cm. These data were used to estimate production and standing crop biomass for each plant species from equations developed for these plots (Alaback 1980).

Because attempts to measure light levels under various canopy covers with photocells and chemical light meters (Friend 1961) were unsuccessful, an indirect index of light interception was derived by estimating tree canopy cover. At the center of each 4-m² plot cluster, four measurements of canopy density were made with a spherical densiometer (Strickler 1959). These data were used to estimate percentage of canopy cover and variance for each quadrant of the cluster. Understory-overstory relationships were further characterized by measuring the distance from the plot center to the nearest tree >2.5 cm in diameter in each of four quadrants, as well as the diameters of the four trees (Cottam and Curtis 1956).

Overall plot aspect, slope, shape (convex, concave, or flat) and physiographic position (midslope, ridgetop, marine terrace, alluvial flat) were recorded. Plot elevation, latitude, and longitude were taken from 15′ topographic maps issued by the United States Geological Survey. An aneroid altimeter was used when elevation could not be accurately estimated from the maps.

RESULTS

Seventy-eight species of plants occur on the 60 sites sampled in this study, including 27 species of bryophytes and lichens, 11 species of shrubs, 35 species of herbaceous vascular plants, and 5 tree species. The majority of these species are restricted geographically or with respect to microenvironment or disturbance history. Within each study site, bryophytes, especially the liverworts, are more restricted by substrate and microclimate than are vascular plants.

Over 70% of the ground cover is occupied by the 10 most abundant species, each of which generally occurs on 90% or more of the sites (Table 2). The feather mosses (*Rhytidiadelphus loreus, Hylocomium splendens*) are the most widespread, occurring in virtually all of the sites. In contrast, most of the herbaceous vascular plants are restricted by stand age class or disturbance history.

General successional trends

Sampling indicated that shrubby and herbaceous vegetation as well as tree seedlings respond quickly to the more favorable growth conditions created by overstory removal (Fig. 2). During the 1st 20 yr after logging, production of shrubs and herbs increases linearly with time (Fig. 3). Decreased competition with conifers, increased light, more favorable temperatures, and nutrient availability all undoubtedly play a role in stimulating this growth (Likens et al. 1978). A decline and recovery in flowering plant production after disturbance (Bormann and Likens 1979) is completed in <3 yr; one stand of that age attained levels of herb and shrub production comparable to that of old-growth forests (Table 1). By age 20 yr, production can increase to as much as 5.2 Mg·ha⁻¹·yr⁻¹.

Most of this regrowth represents a response of the woody shrub species. In the Maybeso Valley (plot 52), for example, nearly impenetrable shrub thickets have developed because soil disturbance is higher and tree density lower than in surrounding clearcuts. *Vaccinium* spp. in combination with *Rubus spectabilis* and *Ribes laxiflorum* represent an average of >90% of the understory production in young southeast Alaska forests. Tree seedlings (<2.5 cm in basal diameter) follow a pattern similar to that of the woody shrub species (Fig. 4).

The other understory strata have varying responses to overstory removal (Table 1). *Dryopteris* and *Blechnum* ferns generally develop in dense clumps when tree regeneration is sparse. *Dryopteris* dramatically increases in biomass in young stands, frond lengths often exceeding 1.0–1.2 m (compared to 0.1–0.3 m in mature forest). These ferns tend to decline later as *Vaccinium* and *Rubus* form an increasingly dense canopy layer with tree saplings 20–25 yr after cutting. In most stands, low shrubs and herbaceous phanerogams decline shortly after forest cutting (Fig. 5). Herbaceous vegetation is often negatively influenced by the growth of woody shrubs during this stage. On areas with heavy soil disturbance, for instance, *Rubus spectabilis* frequently forms a dense canopy cover with only scattered *Hylocomium* and *Rhytidiadelphus* feather mosses and leaf litter beneath.

The lignified or dead woody components of understory vegetation steadily increase during the 1st 5–10 yr after logging. Consequently, by the time shrubs are shaded out by the tree canopy, succulent tissues (young twigs and deciduous leaves, or the annual production)

TABLE 2. Occurrence of understory plant species on the 60 study plots. Only those species are included that constituted >0.1% of the vegetative cover of the study plots.

Class and species	Cover* (%)	Production* (%)	Cover rank†	Constancy‡ (%)
A. Bryophytes and lichens				
Cladonia coniocraea	0.5	+	33	41
Dicranum fuscescens	1.8	0.8	10	94
Foliose lichens§	0.8	+	26	77
Hookeria lucens	0.2	+	40	26
Hylocomium splendens	11.4	7.7	2	97
Isothecium stoloniferum	0.6	+	31	62
Jungermanniales spp.	3.3	0.5	7	86
Marchantia polymorpha‖	0.6	0.3	32	30
Plagiothecium undulatum	3.7	0.6	5	97
Pogonatum macounii	0.7	0.1	27	68
Polytrichum spp.¶	0.5	+	34	44
Porella navicularis	1.8	+	13	86
Rhizomnium glabrescens	7.0	2.8	4	92
Rhytidiadelphus loreus	25.0	11.2	1	96
Sphagnum spp.#	1.6	1.2	14	61
Stoksiella oreganum	0.9	0.3	23	41
Timmia austriaca	0.2	+	41	23
Other mosses**	1.6	0.5	15	70
B. Conifers				
Picea sitchensis	0.9	3.3	22	47
Thuja plicata	0.2	0.5	42	11
Tsuga heterophylla	2.9	18.0	9	89
C. Ferns				
Athyrium felix-femina	1.2	0.3	19	38
Blechnum spicant	0.6	0.1	29	26
Dryopteris austriaca	3.6	0.8	6	85
Gymnocarpium dryopteris	3.0	0.2	8	71
Lycopodium annotinum	0.1	+	47	11
Thelypteris phaegopteris	0.1	+	46	6
D. Shrubby flowering plants				
Gaultheria shallon	0.2	+	43	9
Menziesia ferroginea	0.1	0.8	21	55
Oplopanex horridum	0.9	+	25	29
Ribes laxiflorum	0.3	+	47	6
Rubus spectabilis	2.6	19.1	10	39
Sambucus canadensis	0.1	+	45	11
Vaccinium alaskaense	8.4	5.0	3	88
Vaccinium parvifolium	1.2	1.9	20	91
E. Herbaceous flowering plants				
Coptis asplenifolias	0.9	+	24	38
Cornus canadensis	1.5	0.5	16	61
Maianthemum dilatatum	0.7	0.1	28	46
Moneses uniflora	0.6	+	30	61
Rubus pedatus	2.0	+	11	59
Streptopus amplexifolius	0.4	+	36	30
S. roseus	0.3	+	37	30
S. streptopoides	0.5	0.2	22	47
Tiarella trifoliata	0.2	+	18	70
Viola glabella	0.1	+	44	12

* Mean % of vegetation encountered in this study. + indicates <0.1% production.
† 1 = highest % ground cover, 57 = lowest % ground cover.
‡ % of study sites for which the species was recorded.
§ Primarily *Lobaria oregona* and *Peltigera canina*. Also *Sphaerophorus bulbosus* and *Hypnogymnia enteromorpha*.
‖ Also includes *Conocephalum conicum*.
¶ *P. juniperinum* and *P. commune*.
# *S. squarrosus* and *S. girgensohmii*.
** *Plagiothecium elegans*, *Ptilium crista-castrensis*, and *Hypnum* spp.

FIG. 2. Peak understory production for the chronosequence, with shrubs dominating understory biomass: plot 52, Maybeso Valley, stand age 20 yr.

FIG. 4. Changes in forest structure over time. (Top) Average percentage of canopy cover and variance in mean; plots with similar variances are shown by the same point. (Bottom) Tree foliage and aboveground seedling biomass. Foliage biomass estimates were derived from samples in the Pacific Northwest and tend to overestimate the values but not the pattern of biomass accumulation for trees of the size range commonly found in Alaska.

are a minor component of the understory. The peak in understory biomass production and accumulation occurs at $\approx$15–20 yr after logging. Standing crop biomass declines more slowly than annual production after 20 yr because of the high percentage of woody material (Table 1).

The 20–30 yr age class encompasses the most dynamic stages of understory development. A dense overstory canopy generally develops during the latter part of this period (Figs. 4 and 6). Slight differences in environmental parameters or forest structure generally result in large differences in understory growth during this stage. At Tuxekan Island, for example, two plots that were part of the same clearcut 31 yr ago

have similar soil structure and parent material but differ in tree-growing potential (site index) by 8 m. Plot 24, near sea level, consists of a slowly developing Tsuga-dominated forest with a well-developed but highly clumped woody understory having a biomass of >5.5 Mg/ha (Table 1). Plot 27, 60 m higher in elevation, consists of a fast-growing spruce-dominated forest with only 6% as much understory biomass as plot 24. Tree basal area is twice that of the lower plot, and canopy closure is more complete.

Tree site index is not clearly related to patterns in

FIG. 3. Accumulation of aboveground biomass in the understory over time. Bars represent 95% confidence limits; n = 40–60 for each study plot. Plots with anomalous soil morphology are not included.
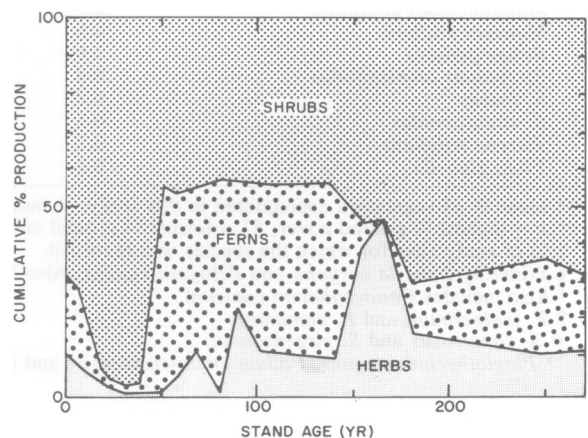
FIG. 5. Structural changes in the understory over time. Based on mean values of annual production by 10-yr age classes.

FIG. 6. Peak (or post peak) biomass of *Rubus* and *Vaccinium* during canopy closure: plot 48, Shrubby Island, stand age 27 yr.

FIG. 7. Depauperate understory dominated by *Rhytidiadelphus* and *Hylocomium*: site 31, Saks Cove, stand age 58 yr.

understory development over the full chronosequence. Within younger age classes, however, high site index is consistently associated with earlier canopy closure. Thus, less dry matter production in the understory would be expected over the early successional stages in stands with a high site index and normal tree density.

After canopy closure, understory production normally stays below 0.1 Mg·ha^{-1}·yr^{-1} for ≈100 yr. A decline in both standing crop biomass and annual production of the understory generally occurs during this period. This decline is primarily related to the elimination of *Rubus spectabilis* and *Vaccinium alaskaense* as the canopy closes. During this successional stage, small, decumbent evergreens (*Vaccinium parvifolium, Moneses uniflora*) and leafy liverworts (Jungermanniales) persist beside root mounds and logs or tree stumps. Clumps of rhizomatous ferns, such as *Gymnocarpium dryopteris* and *Dryopteris austriaca,* occur on both decaying wood and duff layers on the forest floor.

Particularly prominent after canopy closure is the formation of extensive carpets of mosses, especially *Rhytidiadelphus* and *Hylocomium* (Fig. 7). By 50 to 70 yr, these feather mosses form layers over all but the most recent logs as well as the forest floor, greatly exceeding the biomass of understory vascular plants.

At 50 to 60 yr, *Dryopteris, Gymnocarpium* and, in some forests, *Blechnum* ferns begin to dominate understory production of vascular plants. The dominance of ferns over herbs forms a distinct phase in the successional development of the vegetation. Accumulation of moss biomass increases significantly until

≈150 yr after logging or fire (Figs. 5, 8). It peaks at 140–160 yr on a variety of forests in both the Petersburg and Juneau regions. Thereafter, moss biomass declines as shrub and herb components increase during the last stages of successional development. Tree growth also declines after the first century as losses to mortality and fungal attack become more significant (Taylor 1934, Laurent 1974).

The final stages of understory development (Fig. 9) represent a transition to the dynamic equilibrium of an old-growth forest dominated by *Tsuga heterophylla* of climax structure (Whittaker 1953). In these forests dominant trees generally exceed 250 yr of age, and there is a wide range of tree size classes as well as forest floor substrates and microenvironments in which understory plants may grow. Decaying wood generally increases over time so that it becomes more conspicuous than in rapidly aggrading, even-aged forests. The enlarged bases of the oldest trees (200 cm or more in diameter) tend to favor growth of herbs and low shrubs on *Rhytidiadelphus* mats. The more heterogeneous canopy of these older forests apparently allows for greater development of epiphyte biomass and diversity, as has been documented elsewhere in the Pacific Northwest (Pike et al. 1975, 1977). *Lobaria, Hypnogymnia, Sphaerophorus, Usnea,* and *Peltigera* are particularly common as fragments blown from the canopy or as actively growing thalli on the forest floor.

Biomass of tree seedlings (*Tsuga heterophylla, Thuja plicata*), like that of other vascular plants in the understory, increases during the final successional stage. During this period, most tree seedlings are con-
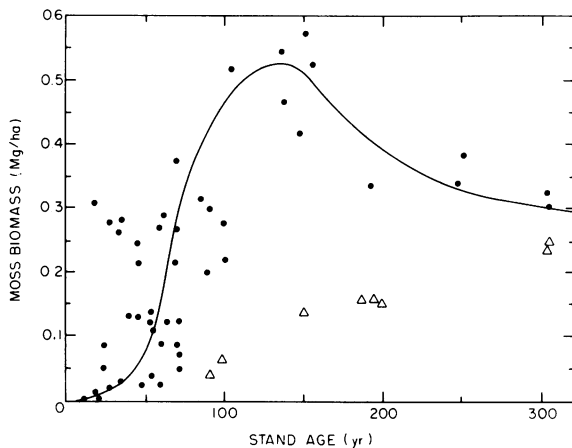
FIG. 8. Bryophyte successional patterns. Sites with significant overstory disturbance from windthrow are indicated by triangles.

FIG. 9. The old-growth stage in which a vascular understory has been reestablished, especially *Vaccinium* and *Tsuga*: plot 38, Clark Bay, stand age 192 yr.

centrated on well-decayed logs and stumps (decay class 4 or 5 of Fogel et al. [1974]). Understory plants are variably spaced under old-growth forests. In some stands, *Vaccinium* develops a nearly continuous stratum. In others, shrubs form distinct clumps around the edge of logs, root mounds, or stumps. Uneven-aged old-growth forests thus differ both structurally and functionally from younger even-aged forests and are generally more heterogeneous than any other age class (Franklin et al. 1981).

Understory dynamics in relation to environmental factors

For this study, understory growth was considered a function of six main factors: competition for light, competition for belowground resources, past disturbance, pattern of tree regeneration, soil characteristics, and microclimatic effects. The relationships of each of these factors to understory growth are summarized in the following sections.

Competition for light.—Forest structure is generally thought to influence understory vegetation by altering microclimate. In a wet maritime climate at low elevations, high moisture availability and a low level of temperature variation would not normally be considered good predictors of understory growth. The most dramatic change observed in the microclimates of these stands over the chronosequence was the change in light reaching the forest floor. Light was therefore chosen as the key environmental factor to be studied in relation to understory growth.

Densiometer readings of tree canopy cover were used as indices of light interception. Percentage of canopy cover was found to have a significant negative relationship with understory development during the first 100 yr ($r = -.7$, $\alpha = .01$). Most plots, however, had canopy covers exceeding 90%; consequently, most of the understory variation explained by canopy cover was associated with the few plots with open canopies (Fig. 10). For this reason, little relationship was found between canopy cover and understory growth in the older age classes. The variation in understory productivity by canopy density class limited the usefulness of this approach to studying canopy-understory relationships.

As an alternative index of canopy density and thus of light interception, the biomass of tree foliage was regressed against understory production. The relationship between these two variables was weaker ($r = .58$) than that between understory production and canopy cover, suggesting that the understory may be responding to other environmental variables. Previously reported high correlations of understory growth and foliar biomass or leaf area of the overstory are perhaps applicable only to rapidly aggrading systems in which these variables are better correlated with the operational factors governing understory growth.

Tree basal area is often used as a predictor of understory biomass. For the study plots, basal area by itself was not as precise a predictor of understory biomass as either percentage of canopy cover or foliar biomass.

Competition for belowground resources.—A second factor influencing understory growth is competition between trees and the understory for nutrients and other belowground resources. The rate of nutrient and water uptake by trees should be related to their growth rate. If the understory is influenced by tree competition unrelated to canopy structure, tree growth as indexed by wood production should be negatively relat-
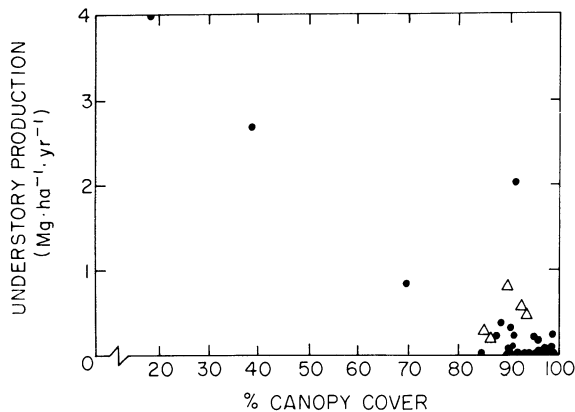
FIG. 10.   Relation of canopy cover to understory production. Young-growth stands on anomalous soils (see text) are not shown. Stands >150 yr old are indicated by triangles.

ed to understory production. However, analysis revealed little negative correlation between wood production and understory production for plots aged 30–150 yr. At Youngs Bay (plot 66), a well-developed understory producing 0.7 Mg·ha⁻¹·yr⁻¹ persists despite high wood production (5.5 Mg·ha⁻¹·yr⁻¹). The lowest levels of tree production occur on two stands with low site indices and little understory production: <0.1 Mg·ha⁻¹·yr⁻¹ for the 72-yr-old plot and 0.7 Mg·ha⁻¹·yr⁻¹ for the 138-yr-old one.

Taylor (1934) estimated peak wood production for low-elevation *Picea-Tsuga* forests in southeast Alaska at ≈70 yr, with production declining gradually to the old-growth stages. In the present study, wood production varied significantly in each age class because of differences in site index and tree density (basal area). The decline in tree vigor and production in the 100–150 yr age class may be related to the increased understory development during this period, but this supposition is not supported by the data on wood production (diameter increment). When more detailed data on such factors of forest production as foliar and branchwood production, respiration, mortality, and especially, belowground carbon assimilation become available, these relationships can be more thoroughly evaluated.

Past disturbance.—The type of past disturbance in the stand, particularly that which eliminated the previous forest, is an additional factor influencing the succession of understory vegetation. In other studies (Odum 1960, Dyrness 1973, Bormann and Likens 1979), this variable has been shown to have a profound influence on species composition and structure, often determining the long-term pattern of successional development. In southeast Alaska, however, the mild, wet summers, the rarity of catastrophic fire, the relatively depauperate flora, and the high percentage of residual

plants persisting after the destruction of the old-growth forest minimize the impact of past disturbance on succession. Some annual "ruderal" species (Grime 1979) do colonize recent clearcuts and burned areas in the region, but they are not a significant component of understory biomass on any of the study plots.

No clear differences in understory development were noted after harvesting with various cable logging systems (A-frame, hi-lead, skyline). Tractor logging tends to be more destructive, however, and when done on fragile beach soils may substantially alter their nutritional and physical structure, thereby retarding successional development (Froehlich 1978). Clearcuts with the greatest degree of topsoil disturbance or mass-movement erosion tend to favor colonization by shade-intolerant species such as *Rubus spectabilis*. Clearcuts in which topsoil disturbance is minimal tend to favor reestablishment of those species present in the original forest, such as *Vaccinium Alaskaense* and *V. parvifolium*. These patterns of early succession are consistent with those observed elsewhere in coniferous forests (Kellman 1969, Dyrness 1973).

Plot 41 at Douglas Island developed a productive and diverse understory a full century before most other forests did so. The history of this stand is unique and helps explain this anomalous understory. During the early 1900's when most of the trees were established, Douglas Island was a center of mining activity. Sulphur fumes and mining tailings eliminated the original forest and retarded tree reestablishment (Muir 1915, Schoephorster and Furbush 1974). After 64 yr, understory production was over four times that measured for other plots in this age class and well distributed among ferns, herbs, and shrubs (Table 1). The tree canopy was more open and the tree basal area was only 69% of that expected for a stand of this age and site index (Taylor 1934).

The only type of past disturbance associated with a change in the long-term pattern of understory development is windthrow. Most young-growth forests of windthrow origin have thin soils and significant slopes, which are associated with greater understory production than exists on other stands of the same age. In contrast, stands subjected to windthrow >140 yr ago have less than normal understory development. At Clark Bay (plots 37, 38), 52-yr-old *Tsuga* saplings have formed a distinct stratum beneath the 190-yr-old dominant trees so that few herbs or shrubs occur on the forest floor. Other stands >100 yr old and apparently subject to periodic windthrow do not have so obviously altered a forest structure except for their diameter distributions and diverse canopies. All of these stands are distinguished from others in their age class by having understory production similar to that of young-growth stands of the same tree basal area (Fig. 11).

When the canopy is disturbed by windthrow during the aggradation phase of succession, understory pro-
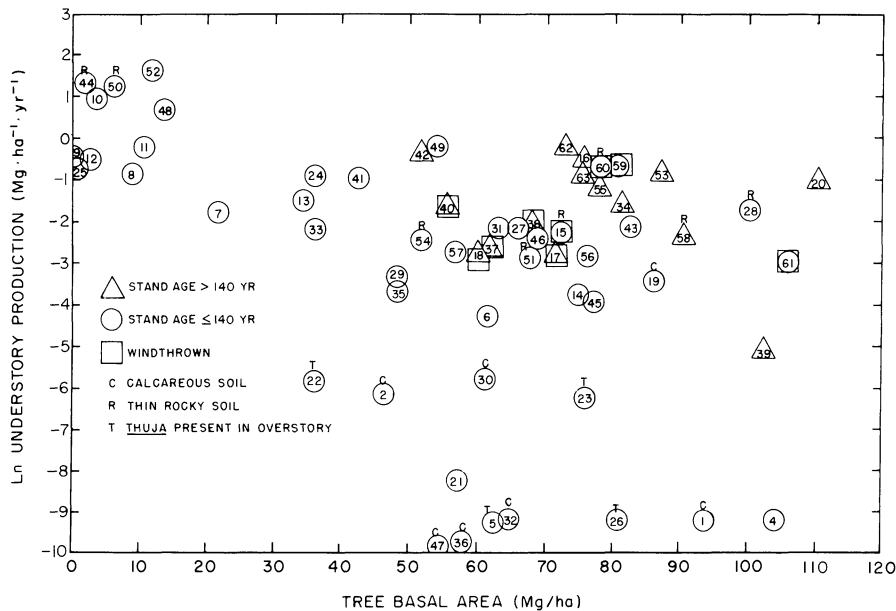
FIG. 11. Relation of tree basal area to understory production on various study plots identified as to age, origin, and soil.

duction is generally stimulated, probably by increased light. If windthrow occurs periodically, leaving enough canopy dominants to maintain stand integrity during the transition or old-growth phase, secondary *Tsuga* or *Thuja* canopy layers generally develop. This denser canopy is associated with decreased understory growth. Thus, windthrow can either enhance or degrade the understory environment, depending on the intensity of disturbance, periodicity, and stand age.

Pattern of tree regeneration.—Another factor affecting understory dynamics is the pattern of tree regeneration after stand disturbance. Coniferous forests in southeast Alaska differ from most forests in the western United States in having abundant natural regeneration of trees within 2–3 yr after disturbance. The persistence of residual *Tsuga* seedlings and saplings can be particularly effective in such regeneration.

Increased densities of tree seedlings are associated with large decreases in understory production. Excluding one plot in the Maybeso Valley, 81% of the variation (α = .005) in understory production on stands measured prior to canopy closure can be explained by knowing the tree density. When plots close to the one at Maybeso and with the same slope, aspect, elevation, and soil type were sampled, they had much lower understory production. This discrepancy may have been caused by the severe disturbance of the Maybeso plot when it was logged (Harris 1974) or by its noted increase in mass-movement erosion (Swanston 1970).

Only in the extreme case of tree establishment being significantly delayed could the pattern of regeneration have a long-term effect on understory succession. Even

in contrasting environments at Harris River and Maybeso Valley, for example, canopy closure should still occur within 10 yr, producing similar understory structures over the next century (Taylor and Godman 1950).

Soil characteristics.—Although canopy structure and past disturbance account for most of the variation in understory biomass over the chronosequence, soil characteristics are also involved. Covariance analysis (Draper and Smith 1966) indicated that 10–20% of the residual variation in understory production can be accounted for by soil type, after variation associated with tree basal area and canopy cover is accounted for (Table 3). As expressed in the soils classifications of Stephens et al. (see footnote 2), thin and rocky (F2n), somewhat poorly drained (F4c), alluvial terrace (F1t), and uplifted beach (F1b) soils are associated with biomass values divergent from those for understory on modal soil types (F1n).

The effect of soil characteristics on shrub and herb development is most pronounced during the earliest stages of succession, prior to tree canopy closure. Twenty-yr-old forests on uplifted beach soils (F1b, Saltchuck series), for example, tend to have above-normal understory production. These forests are most susceptible to disturbance during logging and tend to have lower densities (basal areas) of trees after logging than those on better developed soils. In contrast, forests on moderately to poorly drained soils tend to have lower levels of shrub and herb biomass. On these forests, shrubs and trees take longer to develop continuous strata than on modal soils (F1n). After canopy closure, forests on moderately to poorly drained sites

TABLE 3. Covariance analysis of understory with respect to overstory and environmental variables.

Data set†	n	Covariate	Slope	r^2	Other independent variables	Full model r^2	Full model Significance
Overstory variables							
F	57	age	−	.023	% canopy***, foliar biomass, canopy variance**	.56	.010
F	57	age	−	.023	basal area***, volume, density	.40	.050
YG	33	age	−	.360	% canopy***, foliar biomass*, canopy variance	.67	.000
M	23	age	+	.69	basal area, density index, volume	.73	.000
M	23	age	+	.69	dbh*, variance in dbh, volume	.79	.000
M2	24	dbh	+	.22	% canopy*, variance in canopy, aspect***	.60	.005
Environmental variables							
YG	33	age	−	.36	aspect, slope, latitude	.37	.050
M	23	age	+	.69	aspect, latitude*, slope	.81	.000
YG	33	% canopy	−	.58	physiography	.70	.000
M2	24	dbh	+	.22	soil type	.53	.050
M2	24	dbh	+	.22	parent material*, physiography	.66	.050
YG2	37	basal area	−	.60	volume, soil type	.71	.000

  † F = full data set minus plots on anomalous soils (25, 41, 50); YG = young growth (<90 yr) minus plots 9, 12, 25, 41; M = mature and old growth minus plots 60, 66; M2 = all mature stands minus plot 15; YG2 = all stands <90 yr.
  * = significant at α = .05.
  ** = significant at α = .01.
  *** = significant at α = .005.

maintain a particularly dense canopy and associated depauperate understory.

Soil differences are also associated with anomalies in understory structure during the later stages of succession. The most dramatic differences in understory growth and composition are found on thin, rocky soils (F2n, Tolstoi). Most stands sampled on these shallow soils have understory production significantly above average. Second-growth stands on F2 soil types generally have above-average shrub production but are low in herbaceous production, as are second-growth stands on deeper soils (Table 1).

The remaining plots with abnormal understory growth have anomalous soil structure. Soils that developed on calcareous materials (limestone, marble) are associated with second-growth forests having below-average understory production. Calcareous areas with good internal drainage, gentle slopes, and deep soils tend to have the highest tree growth potential in the region (Godman 1952). Such areas tend to develop a dense basal area stocking of trees, and thus a dense canopy, which leads to unfavorable growing conditions for the understory.

Forests growing on river alluvium also have abnormal understory structures. Understory productivity in these forests is related to depositional history and water table fluctuations. Well-drained alluvium with open park-like forests dominated by *Picea* tends to accumulate the highest shrub biomass.

Covariance analysis revealed that the soil characteristics best related to understory development are qualitative variables (i.e., soil type). Soil depth, texture, color, and structure are not clearly related to understory growth, even though they are used to de-

fine soil types. The lack of an identified understory response to these factors may be related to the nonlinear character of the response, as well as to important interactions between these variables and understory growth.

Microclimatic effects.—The effects of microclimate on understory growth over the chronosequence were assessed by determining percentage of slope, aspect, latitude, and physiographic type for the various plots within each age class. Among the physiographic types sampled, understory growth deviated from the mean most significantly on midslopes, ridges, alluvial terraces, and beaches, after the understory variability associated with tree canopy cover was taken into account. Most of the younger forests (100 yr old or less) sampled had gentle slopes and occurred at similar elevations. The 10 plots with significant slopes (20–47%) and aspects in this age class did not have understory production significantly different from the mean except when thin, rocky soils were also present (plots 54, 60).

In contrast, data on the older age classes suggest that slope, aspect, and physiographic type can be related to changes in understory growth and structure (Table 3). In these age classes, a broader range of slopes and aspects was sampled because there were fewer flat, well-drained, undisturbed plots. On older plots, slope was significantly correlated with increased understory production (α = .05). Northern aspects tended to have more understory growth than southern aspects (α = .01).

Such data are difficult to interpret because these variables are not directly related to plant growth but are presumably correlated with other factors that are

so related. These microclimatic variables tend to be significantly associated with each other. The correlation of increased understory growth with side slopes, beaches, and ridgetops can be interpreted, for instance, as reflecting the importance of thin soils (on ridgetops), soil parent material and genesis (on alluvial terraces and uplifted beaches), and slope.

The pronounced tendency toward increased understory growth on north-facing slopes is closely related to decreased forest vigor in these environments. Andersen (1955) and Godman (1952) have suggested that south- and east-facing slopes are best for tree growth in southeast Alaska. Tree basal area and foliar biomass also tend to increase in forests on slopes with southern exposures. *Sphagnum, Leucolepis,* and other bryophytes associated with poorly drained microsites are most common on north-facing slopes. The major beneficial effect of these slopes on the understory is probably the decreased competition from trees, rather than the microclimate itself.

The effects of environment on understory growth as suggested by this study confirm those described by Siccama et al. (1970) for the northern hardwood region, Zobel et al. (1976) for the west-central Cascades of Oregon, and Daubenmire (1978) for the North American continent: those factors leading to less favorable growing conditions for trees tend to be associated with increased understory production and diversity.

Discussion

Comparison with other forest types

It is difficult to compare the dynamics of understory biomass in southeast Alaska with that observed in other temperate regions. First, few studies have been conducted on this subject. Second, in such studies there is a lack of standardization and, in some cases, of documentation of methods or definitions employed. Nevertheless, comparison of estimates of understory biomass from this study and from other adequately documented studies should reveal how successional patterns in coniferous forests of southeast Alaska differ from and resemble those in such forests elsewhere.

Published values for shrub and herb biomass in coniferous forests prior to canopy closure range from 39.1 Mg/ha in nearby British Columbia (Webber 1977) to 2.0 Mg/ha in England (Ovington 1962). In comparison with coniferous forests of Europe (Ovington 1962), most plots measured in southeast Alaska have high shrub biomass (one reaching 58.5 Mg/ha), but most are within the range reported for western North America (4.5–39.0 Mg/ha). All published studies consulted on successional dynamics indicated that peak shrub and herb production occurs in the 15–25 yr age class.

After canopy closure, a high production of wood is generally maintained until ≈100–150 yr after forest es-

tablishment (Kira and Shidei 1967, Odum 1969). Most studies of understory biomass have dealt with this age class; published values range from 0.1 Mg/ha in a 41-yr-old, slowly developing *Picea glauca* forest in Minnesota (Alban et al. 1978) to 68.0 Mg/ha in a *Pinus nigra* forest in England (Ovington 1962). The forests of southeast Alaska are apparently distinguished from most other forest types by their lack of understory development during intermediate stages of succession. Understory biomass ranges from 0 to 3.1 Mg/ha, two-thirds of the stands being well below 0.1 Mg/ha (n = 22 stands).

Little information is available on the increase in understory biomass after canopy closure in other coniferous systems. MacLean and Wein (1977) suggest that increased understory development may begin as early as 50–60 yr after cutting in New Brunswick. In the central Oregon Cascades, full understory development has been noted in pure *Pseudotsuga* forests 80–90 yr after cutting. Russel (1974) theorizes that the understory reestablishes itself in as little as 20–40 yr after canopy closure in that region. Clearly, more work should be directed toward documenting understory dynamics late in the successional development of other systems in order to understand canopy-understory relationships better.

In comparing understory structure in different forest types or regions, it is necessary to recognize differences in environments and historical factors that affect successional development. Forests of fire origin in the western United States generally establish tree seedlings slowly because small understory trees seldom persist from the original forest. Dry summers in these areas contribute to an austere seedling environment, further slowing regeneration. Seral intolerant trees, which generally dominate forests under postfire conditions, generally do not form as dense a canopy as the more shade-tolerant species (Drury and Nisbet 1973). In the Oregon Cascades, for instance, mature second-growth forests with pure canopies of single-layered *Pseudotsuga* may have a lush herbaceous understory. Adjacent stands will frequently have a multilayered *Pseudotsuga-Tsuga* of even *Thuja* stratum with only a trace of understory development.

In southeast Alaska, on the other hand, *Tsuga,* one of the most shade-tolerant and fire-intolerant western trees (Minore 1979), generally dominates the forest, producing a dense high-leaf-area canopy and a sparse understory. The wet, cool growing seasons in southeast Alaska are apparently conducive to the observed rapid establishment of a dense tree canopy after windthrow or logging. The few studies reporting data on tree canopy coverage and understory biomass confirm that the less rainy climates to the south tend to produce less dense canopies than occur in even the most open (but undisturbed) forests in southeast Alaska after fire or logging (Young et al. 1967, Dodd et al. 1972,

Telfer 1972, MacLean and Wein 1977, Hawk et al. 1979).

Predicting understory biomass

Few models of forest succession have included the dynamics of understory biomass over long timespans. Those that have done so have not given information on relationships between understory growth and canopy structure, relationships vital in characterizing understory dynamics over a range of stand ages and forest structures.

Various authors have attempted to relate understory biomass to tree basal area, percentage of canopy cover, or tree density. Some of these authors have suggested that correlations of understory growth with decreased tree basal area or more open canopies could be used to evaluate the relative importance of direct tree competition and light interception. There are, however, many complex interrelationships between forest structure and understory development. These interrelationships make indirect measures of forest structure, such as tree basal area and percentage of canopy cover, difficult to use as causal factors affecting understory growth.

In order to understand better the nature of these multidimensional interactions between understory growth and forest microenvironment, the relevant parameters must be studied simultaneously. The more salient features of these relationships can be grasped by displaying the study plots on a graph according to their tree basal areas and understory production (Fig. 11). Several plots have below-average understories for their basal areas. Most of these developed on calcareous soils or on areas containing significant amounts of *Thuja* in the canopy. Many of these anomalous plots have denser than average canopies for their basal area classes. The young-growth plots with greater than average understories have developed on thin soils or anomalous soil parent materials, or are of windthrow origin. The only young-growth windthrown plots that do not have above-average understories for their basal areas developed on calcareous soils. These relationships are consistent with the hypothesis of forest vigor and density as the primary controlling factors in understory growth, since calcareous soils and thin rocky soils generally represent the extremes in forest site quality in this region. I hypothesize that tree basal area is important to understory growth during the aggradation phases through its relationship to light interception by the canopy.

The distinctness of the understory environment in the older forests is suggested by the lack of stratification of understory productivity by tree basal area class. In contrast to the younger stands, the indices of increasing tree biomass for older stands, such as mean diameter and volume, are positively correlated with understory growth (Table 3). In older stands, basal area, mean diameter, and volume might be best interpreted as representing the "physiological age" of the forest as it relates to the opening up or diversification of canopy structure. In rapidly aggrading ecosystems, on the other hand, dense, highly productive forests are associated with minimal understory growth. These forests should reach peak overstory production sooner than any other forests and proceed rapidly to a more open, mature canopy structure (Taylor 1934).

Over short segments of successional development, 70–80% of the variation in understory biomass can be related to structural parameters by using multiple regression analysis. Adequate representation of understory changes over longer time periods, however, will require more information on the relationships of these parameters to those factors important to understory growth over the chronosequence. Foremost among those factors to be investigated should be canopy interception, diffusion, and other modifications of solar radiation.

Management implications

The strong pattern observed in understory dynamics over the chronosequence suggests that maintaining the forests of southeast Alaska in the rapidly growing aggradation phases of succession will minimize development of understory vegetation. Under current management practices, forests are maintained on 100-yr rotations. Thus, little accumulation of understory biomass can be expected on the most productive sites during 70–80% of the rotation. On less productive sites, where tree regeneration is not rapid or complete or where subsequent disturbance such as windthrow opens up the canopy, a higher understory biomass can be maintained throughout the rotation.

Annual production of understory biomass in old-growth stands free from windthrow exceeds the production expected from young stands during their entire first century of growth. Animal forage, soil nutrients, and other resources associated with understory vegetation will be minimized in the most productive stands under current management practices, as will the development of the most structurally diverse stage in the region's forest succession. Thinning the overstory canopy may be a possible way to stimulate understory growth under these forests, but until more is known about how the two vegetative layers interact, the development of effective management strategies to encourage the desired understory will be difficult.

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